Contributed Paper

Regional Ontogeny of New England Salt Marsh Die-Off

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Abstract: *Coastal areas are among the world's most productive and highly affected ecosystems. Centuries of human activity on coastlines have led to overexploitation of marine predators, which in turn has led to cascading ecosystem-level effects. Human effects and approaches to mediating them, however, differ regionally due to gradients in biotic and abiotic factors. Salt marsh die-off on Cape Cod, Massachusetts (U.S.A.), triggered by a recreational-fishing-induced trophic cascade that has released herbivorous crabs from predator control, has been ongoing since 1976. Similar salt marsh die-offs have been reported in Long Island Sound and Narragansett Bay (U.S.A.), but the driving mechanism of these die-offs has not been examined. We used field experiments to assess trophic interactions and historical reconstructions of 24 New England marshes to test the hypotheses that recreational fishing and predator depletion are a regional trigger of salt marsh die-off in New England and that die-offs in Long Island Sound and Narragansett Bay are more recent than those on Cape Cod. Predator depletion was the general trigger of marsh die-off and explained differences in herbivorous crab abundance and the severity of die-off across regions. Die-offs in Long Island Sound and Narragansett Bay are following a trajectory similar to die-off on Cape Cod, but are approximately 20 years behind those on Cape Cod. As a result, die-off currently affects 31.2% (SE 2.2) of low-marsh areas in Long Island Sound and Narragansett Bay, less than half the severity of die-off on Cape Cod. Our results contribute to the growing evidence that recreational fishing is an increasing threat to coastal ecosystems and that studying the effects of human activity at regional scales can provide insight into local effects and aid in early detection and potential remediation.*

Keywords: Habitat loss, historical ecology, human impacts, trophic cascade

Ontogenia Regional de un Incremento en la Mortandad en una Marisma Salada de Nueva Inglaterra

Resumen: *Las zonas costeras se encuentran entre los ecosistemas más productivos y más afectados del mundo. Los siglos de actividad humana sobre las líneas costeras han ocasionado la sobreexplotación de depredadores marinos, lo que ha llevado a efectos en cascada a nivel de ecosistema. Sin embargo, los efectos humanos y las aproximaciones para mediarlos varían regionalmente debido a los gradientes en los factores bióticos y abióticos. El incremento en la mortandad en una marisma salada en Cape Cod, Massachusetts (E.U.A.), iniciada por una cascada trófica inducida por pesca recreativa que ha liberado a los cangrejos herbívoros del control por depredadores, ha estado sucediendo desde 1976. Se han reportado incrementos similares en las marismas saladas de Long Island Sound y Narragansett Bay (E.U.A), pero el mecanismo que las causa no ha sido examinado. Usamos experimentos de campo para estudiar las interacciones tróficas y reconstrucciones históricas de 24 marismas de Nueva Inglaterra para probar la hipótesis de que la pesca recreativa y la disminución de depredadores son un detonante regional del incremento en la mortandad de las marismas saladas en Nueva Inglaterra y que los incrementos en Long Island Sound y Narragansett Bay son más recientes que los de Cape Cod. La disminución de depredadores fue el detonante general del incremento en mortandad de las marismas y explicó las diferencias entre la abundancia de cangrejos herbívoros y la severidad del incremento a lo largo de las regiones. Los incrementos en Long Island Sound y Narragansett Bay están siguiendo una trayectoria similar al de Cape Cod, pero están aproximadamente 20 años atrás del de esa localidad. Como resultado, el incremento en la mortandad actualmente afecta 31.2% (SE 2.2) de las áreas de marismas bajas en Long Island Sound y Narragansett Bay, menos de la mitad de la severidad del incremento en Cape Cod. Nuestros resultados contribuyen a la creciente evidencia de que la pesca recreativa es una amenaza que va en aumento para los ecosistemas costeros y que el estudio de*

los efectos de la actividad humana en escalas regionales puede proporcionar una introspectiva a los efectos locales y auxiliar en la detección temprana y la remediación potencial.

Palabras Clave: cascada trófica, ecología histórica, impacto humano, pérdida de hábitat

Introduction

For millennia coastal marine habitats have been among the most heavily affected ecosystems worldwide (Lotze et al. 2006). Nearly 50% of the human population live within 200 km of a coast (MEA 2005), a population trends that has led to widespread ecological problems, including eutrophication (Vitousek 1994), pollution (Lotze & Milewski 2004), species invasion (Carlton & Geller 1993), and overharvest of marine resources (Dayton et al. 1995; Jackson et al. 2001). As human impacts on the landscape expand, there is often a temporal lag such that effects occur in some regions earlier than others (e.g., Grosholz 2002; Diaz & Rosenberg 2008). This time lag provides an opportunity to test the generality of the ecological mechanisms behind an ecosystem's response to perturbation. Examining the vulnerability of marine ecosystems to human disturbances by comparing ecosystem response to past and present human impacts across regions is critical for developing a predictive science that can play a major role in conservation and management (Hughes et al. 2005).

Salt marsh die-offs have become increasingly common in the western Atlantic since 1970s and are a model system in which to investigate regional-scale human impacts. First reported in the Canadian subarctic (Jefferies et al. 2006) and since documented in the southeastern United States (Silliman et al. 2005) and Cape Cod, Massachusetts (U.S.A.) (Altieri et al. 2012), salt marsh die-offs are characterized by the loss of foundation plant species to herbivory following human disturbance. On Cape Cod, recreational fishing pressure depletes local predator populations and frees the native herbivorous crab, *Sesarma reticulatum* (hereafter, *Sesarma*), from predator control. In the absence of predators, local *Sesarma* populations increase and crabs denude the low-marsh zone of smooth cordgrass (*Spartina alterniflora*) (Holdredge et al. 2009; Altieri et al. 2012) (Fig. 1a). Die-off is spatially limited to sites accessible to recreational anglers via dredged boating channels or shoreline infrastructure, and neither die-off nor predator depletion has been observed at sites inaccessible to recreational angling (Altieri et al. 2012; Coverdale et al. 2013). Cordgrass loss leads to marsh erosion, and results of historical analyses indicate that die-off and resulting habitat loss on Cape Cod has been increasing in area and intensity for the last 35 years (Coverdale et al. 2013). Recent reports of similar marsh die-offs in Long Island Sound and Narragansett Bay suggest that die-off has become a regional threat to New England salt marshes

(Fig. 1b). With over 80% of Cape Cod low-marsh habitat already lost to die-off, these nascent southern New England die-offs represent a substantial threat to marshes in Long Island Sound and Narragansett Bay.

The southward expansion of salt-marsh die-off provides an opportunity to test the generality of recreational fishing as a trigger of die-off and to investigate local differences in the timing of ecosystem collapse. Specifically, regional differences in current die-off state suggest that predator depletion in New England occurred at different times; predator depletion and increased herbivory occurred earlier on Cape Cod than in southern marshes. Thus, we hypothesized that similar trophic cascades triggered by recreational fishing are causing salt marsh die-off on Cape Cod and in southern New England and that die-off in southern New England is delayed relative to Cape Cod but has consistently expanded since its onset. We predicted that predator depletion and die-off are less severe and *Sesarma* populations lower in southern New England than on Cape Cod. We tested these hypotheses with field experiments and surveys at 24 sites throughout the region in 2011 to elucidate trophic interactions at sites with and without conspicuous die-off (Fig. 1a). We used archived aerial photographs to assess the onset and trajectory of die-off throughout the region over time.

Methods

Study Sites

We conducted field experiments, surveys, and historical analyses at 24 salt marsh sites on Cape Cod (10 sites) and in southern New England (Rhode Island, three sites; Connecticut, four sites; New York, three sites) (Fig. 1a). Field experiments and historical analyses were previously performed at the 14 study sites on Cape Cod (Altieri et al. 2012; Coverdale et al. 2013), but field experiments were repeated at all sites in 2011. All sites were classified a priori as die-off or vegetated on the basis of extent of die-off in 2011 ($n = 7$ per site type on Cape Cod; $n = 5$ per site type in southern New England). Die-off and vegetated sites did not differ between or within regions in elevation ($F_{3, 20} = 0.33$, $p = 0.79$), slope of *Spartina* zone ($F_{3, 20} = 0.60$, $p = 0.62$), creek area ($F_{3, 20} = 0.50$, $p = 0.69$), or total marsh area ($F_{3, 20} = 1.46$, $p = 0.25$), and no sites had permanent freshwater inputs, tidal restrictions, or offshore barriers (T. C., personal observation). We performed surveys and experiments simultaneously across sites using identical protocols and analyzed results
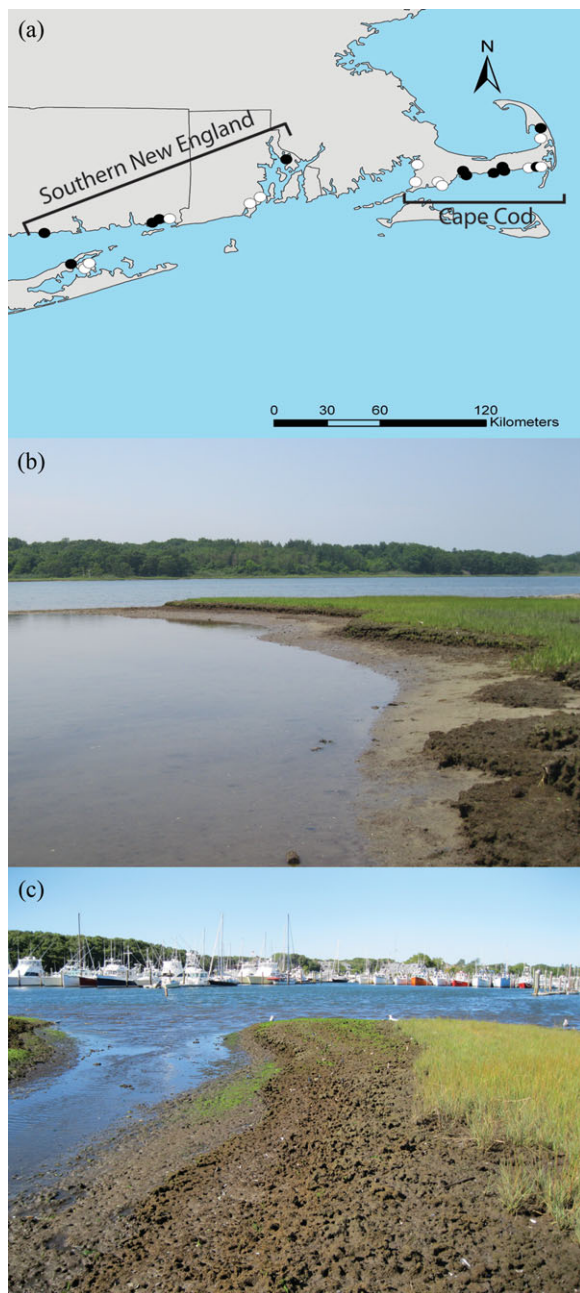
Figure 1. (a) Map of 24 study sites in Cape Cod, Massachusetts, and southern New England (white, vegetated sites; black, die-off sites; sites separated by <5 km in both regions). (b) Typical die-off site in southern New England and (c) Cape Cod, where 30 years of Sesarma herbivory have created 8 m of denuded creek bank.

on both regional (Cape Cod vs. southern New England) and local (vegetated vs. die-off sites) scales.

Recreational Fishing Pressure and Predator Populations

We quantified fishing pressure at southern New England sites with visual surveys of recreational anglers in July 2011. At each site during four separate periods per site ($n = 108$ total survey days), we counted all anglers using rods or hand lines and fishing from shore, docks, or boats. We made observations throughout the day, including within an hour of sunrise and sunset. In July 2010, we performed identical surveys on Cape Cod. Differences in the total number of anglers per site were analyzed with a fully hierarchical analysis of variance (ANOVA) in which site type (vegetated vs. die-off) was nested within region (Cape Cod vs. southern New England).

To examine among-site variation in predator populations, we deployed three baited $30 \times 60 \times 90$ cm traps with funnel openings at each site in August 2011. Traps were constructed of PVC-coated steel mesh and deployed overnight in tidal creeks >100 m apart within each marsh. All individuals caught were identified to species, measured (carapace width for crabs, snout-vent length for finfish, total length for eels) and released alive. We used species- and sex-specific scaling equations to estimate biomass (Hines 1982; Olmi & Bishop 1983; Sachsse 1984; Torchin et al. 2001; Wigley et al. 2003; de Lafontaine et al. 2010) and pooled predators caught in all traps for each site. Only recreationally targeted species reported to consume *Sesarma* and other benthic decapods were included in predator biomass estimates. Nontarget species do not vary between die-off and vegetated sites (Altieri et al. 2012). We analyzed differences in total predator biomass between regions and site types and among sites with a fully hierarchical (nested) ANOVA.

Sesarma Survivorship, Abundance, and Herbivory

In July 2011, we tethered *Sesarma* to assess variation in predation pressure. We secured braided monofilament fishing line to crabs with cyanoacrylic glue and tethered them to metal staples in *Sesarma* habitat at all sites. At each site, 15 crabs were tethered within cages to assess tethering artifacts and 15 were tethered without cages to measure predation pressure. Crabs were deployed for approximately 12 hours overnight and scored for mortality the following morning. Predation mortality left broken carapace fragments attached to tethers, whereas mortality from desiccation left intact dead crabs. Survival in caged treatments was >98% across all sites, indicating minimal effects of handling stress and tether failure on uncaged survival. We analyzed crab survivorship with a fully hierarchical ANOVA with site nested within site type and region.

To quantify differences in *Sesarma* abundance among sites, we deployed pitfall traps in *Sesarma* habitat in August 2011. Traps were 7 cm in diameter and 20 cm deep. At each site, we deployed 12 traps for approximately 12 hours overnight, when *Sesarma* are active. We recorded the number of *Sesarma* in each trap the following morning and then released them at the site of capture. We analyzed *Sesarma* densities with a fully

hierarchical ANOVA with site nested within site type and region.

To assess the effect of elevated *Sesarma* densities on herbivory and cordgrass loss, we examined herbivory on cordgrass transplants and surveyed ambient vegetation for *Sesarma* grazing scars. At each site, eight transplanted culms were deployed for 5 weeks along the active grazing border at die-off sites and at a similar tidal height at vegetated sites. Previous transplant experiments show no effects of transplanting on final cordgrass biomass (Altieri et al. 2012). We collected aboveground biomass from transplants, dried it at 60 ³C to a constant mass, and then weighed it. To assess grazing on ambient cordgrass, 50 randomly selected cordgrass stems within each of eight 1-m^2 quadrats per site were examined for characteristic *Sesarma* grazing damage, including clipped blades and rasped edges (Holdredge et al. 2009). Biomass data from the cordgrass transplant experiment and the proportion of stems grazed from each site were transformed and analyzed with a fully hierarchical ANOVA.

Die-Off Surveys

The area of marsh habitat lost to die-off at each site was quantified in August 2011 along six 100-m transects placed randomly along the low-marsh edge, where cordgrass die-off occurs (Holdredge et al. 2009). For each transect, the vertical width of the die-off area and vegetated low marsh was recorded at eight random points. The total width of the low-marsh zone did not vary between site types or regions, suggesting that die-off width is a function of herbivory intensity rather than site-specific physical factors ($F_{3, 20} = 0.60$, $p = 0.62$). Die-off is easily distinguished by the lack of vegetation and the presence of extensive *Sesarma* burrow complexes, heavily eroded peat, and partially grazed cordgrass stems. To quantify the percentage of the low zone denuded by *Sesarma* grazing, we divided die-off width by total cordgrass zone width (die-off width + vegetated width) and multiplied by 100. We averaged values for each transect and analyzed die-off width with a fully hierarchical ANOVA with site nested within site, type, and region.

Historical Trends in Fishing Pressure and Marsh Die-Off

To investigate the relation between fishing pressure and die-off in southern New England (previously investigated on Cape Cod in Altieri et al. 2012 and Coverdale et al. 2013), we analyzed high-quality aerial photographs of each site. For each site, we acquired a single aerial photograph from each of the following periods: 1930–1949, 1950–1969, 1970–1979, 1990–1999, and 2000–2010. Results of previous work (Altieri et al. 2012; Coverdale et al. 2013) show that fishing infrastructure (docks, piers, boat slips) is an accurate proxy for fishing pressure because most anglers in salt marshes fish from boats or permanent shoreline structures; during our study all anglers observed were fishing from such infrastructure. We used ArcGIS (version 10.1, ESRI, Redlands, California) to georeference historical photographs relative to the most recent photoseries. We plotted the location and extent of vegetated marsh, die-off, and fishing infrastructure for each year and recorded the number of boat slips. We converted spatial maps to raster form with 1-m^2 pixels and tracked the fate of each pixel over time. We analyzed transition matrix data and the number of boat slips with repeated-measures ANOVA (site type and time).

Results

Recreational Fishing Pressure and Predator Populations

Fishing pressure was higher at die-off sites than vegetated sites on both Cape Cod and southern New England ($F_{1, 12} = 30.16$, $p < 0.0001$; $F_{1, 8} = 7.03$, $p < 0.05$, respectively) and was two orders of magnitude greater at die-off sites when averaged across regions (Fig. 2a). Overall fishing pressure did not differ between the two regions ($F_{1, 2} = 0.64$, $p = 0.43$).

Predator biomass was >50% higher at vegetated sites than die-off sites in southern New England, but did not differ between site types on Cape Cod ($F_{1, 2} = 3.74$, $p < 0.05$) (Fig. 2b). Average predator biomass was also higher in southern New England than Cape Cod for both vegetated and die-off sites. Blue crabs (*Callinectes sapidus*) were 96% and 88% of total predator biomass in southern New England and Cape Cod marshes, respectively. Green crabs (*Carcinus maenas*) were also common on Cape Cod, where they were 10% of total predator biomass.

Sesarma Survivorship, Abundance, and Herbivory

Predation rates on *Sesarma* without cages were significantly higher at vegetated sites than die-off sites in southern New England ($F_{1, 2} = 17.1301$, $p < 0.0001$). Predation rates did not differ between site types on Cape Cod, where both site types had significantly lower predation than vegetated southern New England marshes (Fig. 2c).

Sesarma abundances differed significantly between vegetated and die-off sites on both Cape Cod and southern New England ($F_{1, 2} = 64.74$, $p < 0.0001$; population densities were significantly higher at die-off sites than at vegetated sites in both regions (Fig. 2d). Overall, *Sesarma* abundances were approximately five times higher on Cape Cod than in southern New England marshes. No *Sesarma* were caught in vegetated southern New England marshes.

In southern New England, grazing rates on transplanted culms were significantly higher at die-off sites than vegetated sites ($F_{1, 2} = 46.62$, $p < 0.0001$). On
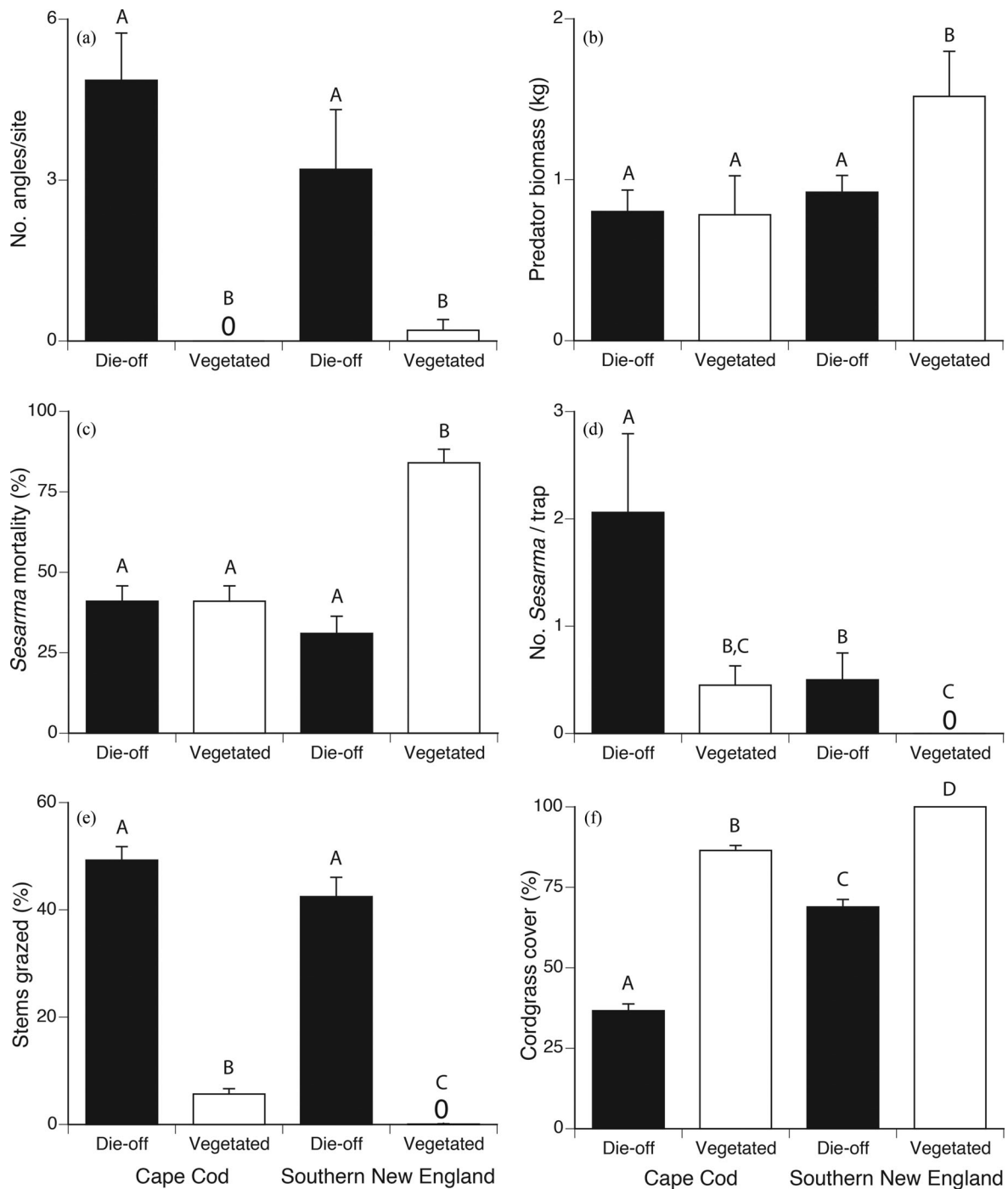
Figure 2. Recreational-fishing-mediated trophic cascades on Cape Cod and southern New England. (a) Mean (SE) total number of anglers per site during surveys (i.e., fishing pressure), (b) predator biomass, (c) tethered Sesarma mortality, (d) number of Sesarma per trap, (e) percentage of stems grazed, and (f) percent cordgrass cover at die-off and vegetated sites. Letters represent results of Tukey's post hoc *analysis.*

Cape Cod, herbivory on transplanted culms was only marginally higher at die-off sites than vegetated sites, but grazing on ambient stems (Fig. 2e) was significantly higher at die-off sites than vegetated sites in both regions ($F_{1, 2} = 559.08$, $p < 0.0001$). Overall grazing rates were higher on Cape Cod than southern New England.

Die-Off Surveys

The amount of low marsh denuded by *Sesarma* grazing was significantly higher at die-off sites in both regions ($F_{1, 2} = 473.59$, $p < 0.0001$). Die-off intensity was significantly higher on Cape Cod than southern New England at both die-off and vegetated sites (Fig. 2f), despite
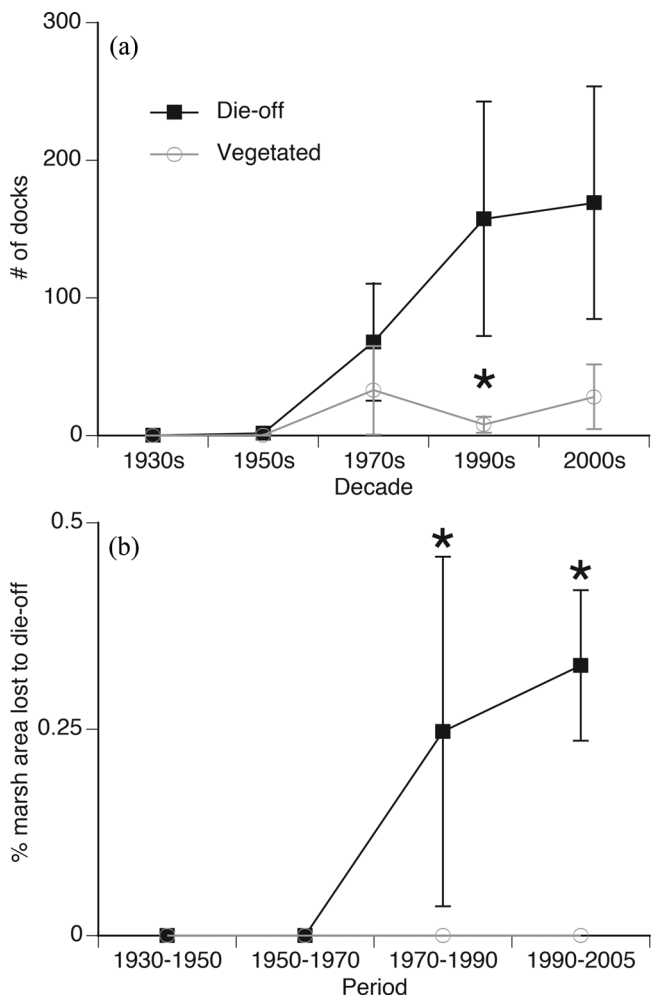
Figure 3. Historical trends (mean [SE]) in the (a) development of fishing infrastructure (*p < 0.05) and (b) resulting marsh loss at vegetated and die-off marshes in southern New England.

Figure 4. Total area (bars) and annual expansion rate (dots) of marsh die-off in southern New England and Cape Cod.

recent widespread recovery of cordgrass at die-off sites on Cape Cod (T.C., personal observation).

Historical Trends in Fishing Pressure and Marsh Die-Off

Die-off sites in southern New England had consistently greater historical and current densities of boat slips ($F_{1, 4}$ = 7.31, $p < 0.0001$, Fig. 3a) than vegetated sites. Similarly, die-off in both regions began after periods of significant coastal development. This development occurred in the 1950s–1960s on Cape Cod, but was delayed several decades in southern New England. Both vegetated and die-off sites in southern New England lost little marsh area to die-off before the construction of marinas and coastal homes in the 1990s. As a result, there was significantly more die-off in southern New England after the 1990s than during the preconstruction period ($F_{15, 24}$ = 3.52, $p = 0.003$) (Fig. 2b). The delayed onset of die-
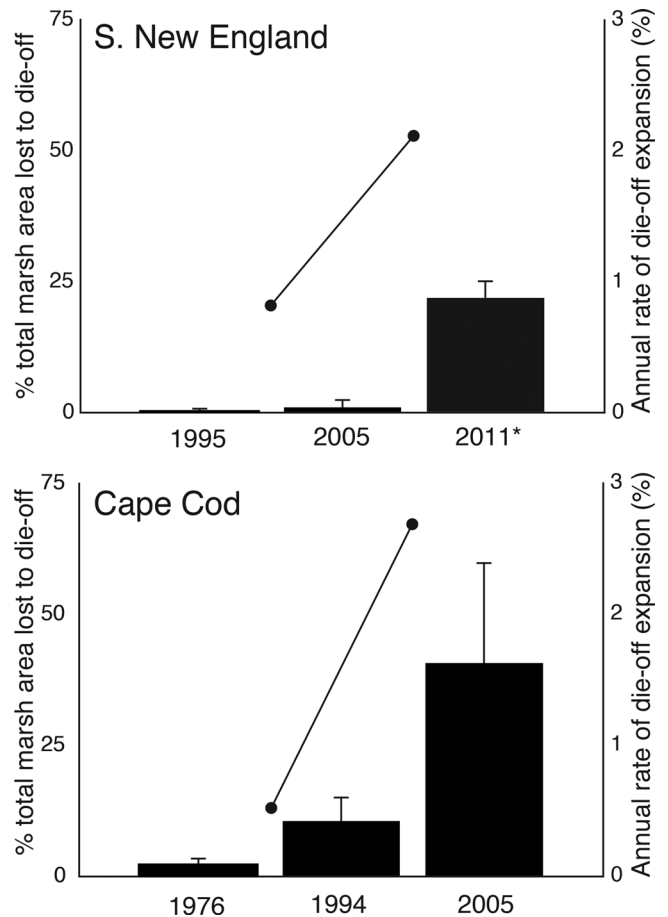
off in southern New England likely explains the lower cumulative loss of marsh habitat to die-off in southern New England marshes. Despite these differences, however, the trajectory of die-off in southern New England over the last 15 years closely paralleled that observed on Cape Cod between 1976 and 2005, where annual marsh loss accelerated following the onset of die-off (Fig. 4).

Discussion

Our results suggest that recreational fishing has led to widespread salt marsh die-off on Cape Cod and southern New England. They also demonstrate how historical data and experimental approaches can be combined to better understand and predict human impacts on ecosystems.

Recreational Fishing and Salt Marsh Die-Off

Tidal elevation, *Spartina* zone slope, creek area, and total marsh area were statistically indistinguishable

between site types, which also did not differ in the presence of major tidal restrictions, freshwater inputs, and offshore barriers. Previous experimental comparisons of nutrient inputs, substrate hardness, flow, nonrecreationally targeted species, and other development-associated disturbances revealed no significant differences between vegetated and die-off sites (Bertness et al. 2009; Altieri et al. 2012). These findings suggest that differences in recreational fishing pressure and the associated loss of top-down control are responsible for the distribution of die-off in both regions.

In southern New England, die-off sites had greater fishing pressure and more fishing infrastructure than vegetated sites. These conditions led to localized depletion of top predators including blue crabs, striped bass (*Morone saxatilis*), and American eels (*Anguila rostrata*). This predator depletion has had cascading effects in southern New England, where predation on *Sesarma* decreased and *Sesarma* densities increased at heavily fished sites, and has led to significantly elevated grazing and the creation of large die-off patches. In contrast, the die-off event on Cape Cod shows signs of a partial recovery, with predator densities and predation pressure at die-off sites rebounding to levels observed at vegetated sites in 2011 (Altieri et al. 2013). This result is in stark contrast to earlier findings on Cape Cod (Altieri et al. 2012), which showed a robust trophic cascade triggering die-off at heavily fished sites as recently as 2010. The short-term recovery of predator populations between 2010 and 2011 at these sites, however, was insufficient to reduce *Sesarma* densities, grazing rates, and die-off extent by 2011 and so represents at most a partial recovery of trophic function. This result is consistent with recent reports of partial cordgrass regrowth at die-off sites, which has occurred despite expansion of die-off elsewhere in the marsh. Regrowth at these sites has occurred mostly at tidal elevations below the foraging range of *Sesarma* and appears to be associated with the recent invasion of predatory European green crabs into *Sesarma* burrow complexes (Altieri et al. 2013; T.C., personal observation).

In contrast, sites lacking historical fishing infrastructure and current recreational fishing pressure supported larger predator populations relative to die-off sites in both regions. At these sites, predation on *Sesarma* was high; there was nearly 100% *Sesarma* mortality of tethered crabs at many southern sites. In the absence of recreational angling, top-down control appears to curb *Sesarma* populations and grazing rates, keeping the low-marsh zone vegetated in both Cape Cod and southern New England. These similarities between marsh die-off on Cape Cod and the more recently reported die-off in southern New England suggest that trophic cascades mediated by recreational fishing are more pervasive than previously thought and have the potential for regional expansion.

Regional Differences in Die-Off Ontogeny and Severity

Despite similarities in trophic patterns at die-off and vegetated sites throughout both regions, several differences between Cape Cod and southern New England marsh die-offs highlight potential regional-scale variation and provide insight into die-off patterns that can inform conservation. Historical reconstructions suggest that die-off in southern New England began approximately 15 years ago, whereas it began over 35 years ago on Cape Cod (Fig. 4). In both regions, however, die-off intensity closely paralleled temporal changes in the construction of recreational fishing infrastructure; die-off began after the construction of docks and marinas and intensified as coastal development increased.

Predator populations also differed in identity, size, and effect between regions. Predator biomass and predation pressure were higher in southern New England than in Cape Cod marshes. Blue crabs represented >85% of predators in both regions, but green crabs were much more common on Cape Cod than in southern New England. Despite lower predator diversity, predation rates were 40% higher in southern New England vegetated sites than Cape Cod vegetated sites, but predation rates were nearly identical at die-off sites. This result reflects regional differences in predator depletion between Cape Cod and southern New England marshes. The severity of predator depletion and loss of predatory control on *Sesarma* was also evident across regions. *Sesarma* densities at die-off sites on Cape Cod were approximately four times higher than at die-off sites in southern New England. Furthermore, although *Sesarma* were detected at both vegetated and die-off sites on Cape Cod, identical trapping methods yielded no *Sesarma* at vegetated sites in southern New England despite evidence of minimal grazing at these sites and the close proximity (<5 km) between interspersed vegetated and die-off sites in both regions.

Understanding the Development of Human Impacts

Together, the results of our historical reconstructions and field experiments suggest that salt marsh die-off in southern New England represents a southward spread of die-off, not a southward spread of die-off reports. The delayed onset of die-off in the region was likely triggered by later construction of coastal infrastructure and greater resilience due to higher overall predation pressure. These regional differences in the onset of die-off are manifested in the striking patterns of predator depletion, *Sesarma* density, and die-off severity between Cape Cod and southern New England marshes.

Despite temporal and biotic lags, however, results of our historical reconstructions suggest that southern New

England marshes are following a similar trajectory to those on Cape Cod, where steadily expanding die-offs caused the loss of >80% of low-marsh habitat and 20% of total marsh area by 2005. Following the onset of die-off, marshes on Cape Cod and southern New England initially lost 0.5–0.8% of their total marsh area to die-off per year within the first 20 years, after which die-off rapidly accelerated in both regions (Fig. 4). Thus, although die-off has had a relatively minimal effect on marshes in southern New England to date, without effective management, marshes in southern New England will likely experience continued expansion of die-off and loss of marsh.

Human impacts on coastal landscapes can fundamentally alter ecosystems such as coral reefs (Hughes et al. 1994), mangroves (Ellison & Farnsworth 2001), seagrass beds (Waycott et al. 2009), and salt marshes (Gedan et al. 2009), but the expansion of anthropogenic regime changes from their epicenter remains underappreciated. Expanding human activity creates natural experiments that allow for the investigation of the mechanisms and consequences of human impacts at regional scales, and studies of ecosystems in all stages of decline are critical to gain the necessary understanding of human impacts necessary to inform conservation and management.

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